

Relative Growth Rates in Three Species of *Desmognathus* (Amphibia: Plethodontidae)

RICHARD C. BRUCE^{1,2}

Department of Biology, Western Carolina University, Cullowhee, NC 28723, USA

ABSTRACT: Observed life histories of animals reflect trade-offs among growth, reproduction, and survival that serve to maximize fitness under particular environmental regimes. Body size and age at first reproduction, as expressions of growth and developmental rates, are key trade-off elements. I estimated relative growth rates in three species of desmognathine salamanders that vary markedly in body size and habitat associations. Sampling was conducted in two assemblages of the species in the southern Blue Ridge of North Carolina. The species, ranked from larger to smaller, were *Desmognathus quadramaculatus*, *D. monticola*, and *D. ocoee*. An existing skeletochronological database served as a source of age estimates in salamanders for which standard lengths had been recorded. Body masses were estimated for these individuals from regressions of mass on standard length. Relative growth rates were estimated by the Gompertz model for growth in standard length and body mass, and by the von Bertalanffy model for growth in body mass only. In young salamanders, higher relative growth rates were recorded in the smaller species; this trend reversed at later ages wherein relative growth rates were greater in larger species over the remainder of the salamanders' life spans. In all three species in both assemblages, the maximum rates of absolute growth in mass occurred near or within the conjoint age range at first reproduction of the two sexes. Body size differences among these species result from differences in propagule size, growth rate, and (as one index of reproductive effort) age at sexual maturation. I present evidence that larger adult body sizes are a product of larger eggs, larger hatchlings, higher rates of growth, and lower reproductive effort in these and other species of *Desmognathus*, in southern Appalachian assemblages of the genus.

Key words: Dusky salamanders; Gompertz function; Growth; Reproductive investment; Skeletochronology; von Bertalanffy function

AMPHIBIANS undergo indeterminate growth in the sense that growth in body size continues into adulthood, gradually slowing after sexual maturation, and eventually approaching an upper limit or asymptote near the maximum size observed in the population in question (e.g., Tilley 1980; Marvin 2001; Lee et al. 2012). Among closely related species, differential selection for optimal body size might involve differential allocation to growth and maintenance, as well as to reproductive traits that directly influence body size, particularly propagule size, fecundity, and age at first reproduction (Roff 2002:Table 4.10). In salamanders, differences in adult body size among syntopic congeners might reflect different life-history strategies for coping with environmental perturbations, as in the sirenids, *Siren intermedia* and *S. lacertina* (Luhring and Holdo 2015), or for exploiting the resources of an environmental gradient, as in *Desmognathus* (Bruce 2011).

Empirical data on growth in amphibians often indicate decaying exponential or sigmoidal patterns of growth that can be approximated by several mathematical models, including the logistic, von Bertalanffy, and Gompertz models (Panik 2014; Martyushev and Terentiev 2015). In a series of papers (Bruce 2009, 2010, 2016), I fitted either or both the Gompertz and von Bertalanffy growth curves to skeletochronological data of three species of *Desmognathus* that vary markedly in adult body size—namely, the large *D. quadramaculatus*, the intermediate *D. monticola*, and the small *D. ocoee*. The original data sets were the basis of studies of age, body size, and population structure of these three species (Castanet et al. 1996; Bruce et al. 2002). All three species were sampled in two nearby watersheds, Wolf Creek in the Cowee Mountains and Coweeta Creek in the Nantahala Mountains, in southwestern North Carolina.

Although the populations of *D. ocoee* in the Cowee and Nantahala Mountains might represent separate species (Bernardo and Agosta 2005), they are more similar in growth, body size, and life history than those of the other two species considered herein, and thus warrant no special consideration.

Plots of body size, either standard length (SL) or mass (M), against age (A) to which growth equations were fitted, showed high levels of residual variance, reflecting variation in growth. Presumably, such variation stemmed from (1) genetic variation; (2) environmental factors, including variation across the years represented by the age ranges of the salamanders, relative to sampling intervals; and (3) size-related differences in survival within cohorts. Also, the growth equations were based on pooled data of the two sexes, given that smaller immatures were not sexed and adult numbers were small in some samples. The point scatters of the plots also incorporated any methodological errors in reading ages from bone sections (Sinsch 2015). For these reasons, I characterized the fitted growth curves as first approximations of the growth of average individuals in the populations under study (Bruce 2010, 2016). From the inflections of the Gompertz equations, I estimated secondary parameters of growth, including age and size at the maximum rate of growth, and the maximum value of the growth rate (Bruce 2010, 2016).

The overall objective of the latter studies was to evaluate the contributions of propagule size, growth, and age at sexual maturation to variation in adult body size among these three species. Larger adult body sizes were attained by *D. quadramaculatus* and *D. monticola* at Coweeta than at Wolf Creek; body sizes of *D. ocoee* were similar in the two assemblages. Although growth rates were higher in all three species at Coweeta versus Wolf Creek, the difference was much less in *D. ocoee* than in either larger species. Within each assemblage, the differences in adult body size among

¹ PRESENT ADDRESS: 50 Wagon Trail, Black Mountain, NC 28711, USA

² CORRESPONDENCE: e-mail, ebruce1563@aol.com

species were attributed to differences in propagule size and age at sexual maturation, as well as to differences in growth rate. Interspecific differences in these traits were considered elements of trade-offs involving growth and body size, reproductive effort, and survival that serve to maximize fitness of larger species in more aquatic habitats and smaller species in more terrestrial habitats (Bruce 2016). Selective factors acting on trade-off combinations in southern Appalachian desmognathines presumably include climatological influences, habitat gradients, resource distributions, predation, and species interactions, including interactions among desmognathine species, as well as between desmognathines and other plethodontids (Hairston 1996; Bruce 2011).

The earlier studies evaluated absolute rates of growth only (dSL_A/dA and dM_A/dA), and did not take into account the body size of the growing individual. Such relative growth rates, formulated as $(dSL_A/dA)/SL_A$ and $(dM_A/dA)/M_A$, would be expected to further explicate the contributions of growth to the differences in body size among these species. Thus, the principal objective of the present study was the evaluation of relative growth rates in the three species, vis-à-vis other factors that contribute to differences in adult body size (e.g., propagule size, age at first reproduction, etc.). Because Gompertz and von Bertalanffy growth models were used in the previous studies (Bruce 2010, 2016), I applied these models in the current study. Given that the point scatters of size against age tended to be sigmoidal, however, I employed the sigmoidal form of the von Bertalanffy function (Panik 2014) versus the decaying exponential form used earlier (Bruce 2010). The skeletochronological estimates of age reported in the previous studies (Castanet et al. 1996; Bruce et al. 2002) served as the database for fitting the relative growth equations. For both the Wolf Creek and Coweeta data sets, I evaluated relative growth rates in SL and body mass from parameters generated by the Gompertz growth model. However, I fitted the von Bertalanffy growth model to the body mass data only. Although the present analysis draws heavily on the aforementioned studies, I found that the results provided additional perspectives of growth phenomena in the three species.

MATERIALS AND METHODS

The original skeletochronological estimates of age were generated by Castanet et al. (1996) and Bruce et al. (2002) for populations of *Desmognathus quadramaculatus*, *D. monticola*, and *D. ocoee* in the Wolf Creek Biology Preserve of Western Carolina University in the Cowee Mountains, and the Coweeta Hydrologic Laboratory in the southern Nantahala Mountains, in southwestern North Carolina. Locality data and methods are given in those papers. Original estimates of age were recorded in years, and later recalculated to the nearest half-month. Growth equations were then fitted to plots of standard length (SL in mm) and body mass (M in g) versus adjusted age (A in years; Bruce 2009, 2010, 2016).

Given that body mass was not measured for the salamanders aged by skeletochronology, I estimated body mass for these salamanders from linear regressions of $\ln M$ on $\ln SL$ in supplemental samples of the three species

(Bruce 2010, 2016). In the current study, I expanded the latter samples for southern Nantahala *D. quadramaculatus* and *D. monticola*. The expanded samples included salamanders from both the Coweeta Creek watershed and the adjacent upper Nantahala River watershed, as described in Bruce (2009). The populations of each species from the two watersheds comprise individuals of essentially equivalent body sizes and proportions. Prior to measurement, salamanders were lightly anesthetized in a 1% solution of MS-222, blotted with paper toweling, and weighed (± 0.001 g). They were then measured for standard length (± 0.1 mm), from the tip of the snout to the caudal end of the cloacal slit. They were rinsed in spring water, revived, and released at the original collection sites.

Estimates of mean standard length at hatching (SL_0) were taken from published sources (Bruce 1990, 2009) and from additional observations at both localities over several years. Given that variances in hatching lengths are low relative to those of standard lengths of older individuals within cohorts, deviations in the estimates of mean SL_0 have only minor effects on the fitted Gompertz curves.

Parameters of the Gompertz function are β_i , the instantaneous rate of growth at the initial size, and α_i , the rate of decay of β_i , for $i =$ either SL or M (Laird et al. 1965). Thus, the Gompertz equation for growth in standard length is

$$SL_A = SL_0 e^{((\beta_{SL}/\alpha_{SL})(1-e^{-\alpha_{SL}A}))}, \quad [1]$$

and the absolute growth rate is given by the first derivative,

$$dSL_A/dA = \beta_{SL} SL_0 e^{((\beta_{SL}/\alpha_{SL})(1-e^{-\alpha_{SL}A}))} e^{-\alpha_{SL}A}. \quad [2]$$

In the current study, I used a simplified version of the Gompertz equation for growth in mass by substituting mean body mass at hatching, M_0 , for the expression $a^{1/b} SL_0$ used originally (Bruce 2010). The resultant equation is

$$M_A = M_0 e^{((\beta_M/\alpha_M)(1-e^{-\alpha_M A}))}, \quad [3]$$

and the solution is identical to the earlier equation. M_0 was estimated from the regression equation, $\ln M_0 = \ln a + b(\ln SL_0)$. The first derivative is

$$dM_A/dA = \beta_M M_0 e^{((\beta_M/\alpha_M)(1-e^{-\alpha_M A}))} e^{-\alpha_M A}. \quad [4]$$

Dividing Eq. 2 and Eq. 4 by body size (either SL or M), in order to generate estimates of relative growth rates, reduces the equations to

$$\left(\frac{dSL_A}{dA}\right)/SL_A = \beta_{SL} e^{-\alpha_{SL}A} \quad [5]$$

and

$$\left(\frac{dM_A}{dA}\right)/M_A = \beta_M e^{-\alpha_M A}. \quad [6]$$

From the Gompertz parameters for growth in SL (Bruce 2009, 2010, 2016) and the revised parameters for growth in mass, I derived estimates of relative growth rates (γ_{SL} , γ_M), as formulated above, from hatching (age 0) to the age where body size equaled or exceeded 99% of asymptotic size. I regressed log-transformed values of the relative growth rate

TABLE 1.—Summary of Gompertz parameters for growth in standard length (SL in millimeters) for three species of *Desmognathus* at Wolf Creek and Coweeta from Bruce (2009, 2010, 2016). The 95% confidence limits are given in parentheses. The values in this table are based on skeletochronological data sets reported in Castanet et al. (1996) and Bruce et al. (2002).

Population	n	SL ₀	β _{SL}	α _{SL}	SL _{max}
Wolf Creek					
<i>D. quadramaculatus</i>	100	13.9	0.517 (0.486, 0.548)	0.269 (0.246, 0.291)	95.0
<i>D. monticola</i>	83	11.8	0.660 (0.625, 0.696)	0.366 (0.339, 0.394)	71.6
<i>D. ocoee</i>	76	9.4	0.648 (0.578, 0.717)	0.377 (0.316, 0.438)	52.7
Coweeta					
<i>D. quadramaculatus</i>	106	14.0	0.489 (0.463, 0.515)	0.243 (0.226, 0.261)	104.7
<i>D. monticola</i>	111	11.8	0.642 (0.600, 0.684)	0.333 (0.302, 0.363)	81.1
<i>D. ocoee</i>	101	9.2	0.696 (0.642, 0.751)	0.388 (0.340, 0.436)	55.5

against age, wherein the intercept of the regression equals $\ln(\beta)$ and the slope equals α of the Gompertz equations.

The sigmoidal form of the von Bertalanffy equation for growth in body mass is formulated as

$$M_A = M_\infty \left(1 - \delta e^{(-\omega(1-k)A)} \right)^{1/(1-k)}, \quad [7]$$

where ω is the growth coefficient, δ is related to the size at birth or hatching, and $1 - k$ is a shape parameter (Fabens 1965; Panik 2014). The curve is sigmoidal for $k > 1$. I initially estimated asymptotic mass, M_∞ , from examination of the plots of mass against age. Then, using the model/loss routine of SYSTAT, I fitted equations to successive approximations of M_∞ until the procedure generated maximum values of R^2 . The absolute growth rate is given by the first derivative,

$$dM_A/dA = \delta\omega M_\infty \left(1 - \delta e^{(-\omega(1-k)A)} \right)^{k/(1-k)} e^{(-\omega(1-k)A)}. \quad [8]$$

Dividing Eq. 8 by body size provides an estimate of the relative growth rate,

$$\left(\frac{dM_A}{dA} \right) / M_A = \left(\frac{\delta\omega}{1 - \delta e^{(-\omega(1-k)A)}} \right) e^{(-\omega(1-k)A)}. \quad [9]$$

As I did for the Gompertz equations, I plotted log-transformed values of the relative growth rate against age for the three species in each assemblage.

To estimate age, λ_i , and size, y_i , at the maximum value of the absolute growth rate, I set the value of the second derivative of the growth equation to zero, representing the inflection, and solved for age and size. For growth in either SL or M of the Gompertz model, the estimates are given by

$$\lambda_i = \ln(\beta_i/\alpha_i)/\alpha_i \quad [10]$$

and

$$y_i = e^{(-1)} y_\infty. \quad [11]$$

For the von Bertalanffy model the corresponding expressions, for growth in mass, are

$$\lambda_M = \left(1 / \left(\omega(k - 1) \right) \right) \times \ln \left((1 - k) / \delta \right) \quad [12]$$

and

$$y_M = M_\infty k^{1/(1-k)}. \quad [13]$$

The relative growth rates at the maxima of the absolute growth rates are α and $\omega(1 - k) / k$ for the Gompertz and von Bertalanffy models, respectively.

All statistical evaluations were carried out with SYSTAT 10 and SYSTAT 12 (Systat Software, Inc., San Jose, CA). I verified calculations of first and second derivatives of the growth equations with Mathematica (Wolfram Research).

RESULTS

Regressions of $\ln(M)$ on $\ln(SL)$ for the three Wolf Creek species and Coweeta *D. ocoee* are given in Bruce (2016:Table 3). For the expanded samples of the other Coweeta species the equations are *D. quadramaculatus*, $n = 77$, $\ln(M) = -10.548 + 2.955[\ln(SL)]$, $R^2 = 0.99$; and *D. monticola*, $n = 50$, $\ln(M) = -10.650 + 2.949[\ln(SL)]$, $R^2 = 0.99$. The high R^2 values (≥ 0.98) in all the regressions lend confidence to the body mass estimates of salamanders aged by skeletochronology.

For all three species, relative growth rates, $\gamma_{SL} = (dSL_A/dA)/SL_A$ and $\gamma_M = (dM_A/dA)/M_A$, based on the Gompertz parameters β_{SL} , α_{SL} , and β_M , α_M (Tables 1, 2), declined monotonically according to the equation $\gamma_i = \beta_i e^{(-\alpha_i A)}$, or, in linear form, $\ln(\gamma_i) = \ln(\beta_i) - \alpha_i A$, for $i = SL$ or M (Table 3; Figs. 1, 2). Early relative growth rates in SL and mass of *D.*

TABLE 2.—Gompertz parameters for growth in body mass (M in grams) for three species of *Desmognathus* at Wolf Creek and Coweeta, based on skeletochronological data sets reported in Castanet et al. (1996) and Bruce et al. (2002). Sample sizes as in Table 1; the 95% confidence limits are given in parentheses. The Gompertz parameters were derived from the simplified equations for growth in mass presented in the text.

Population	M ₀	β _M	α _M	R ²	M _{max}
Wolf Creek					
<i>D. quadramaculatus</i>	0.058	1.751 (1.621, 1.882)	0.313 (0.285, 0.342)	0.90	15.59
<i>D. monticola</i>	0.038	2.086 (1.975, 2.197)	0.409 (0.382, 0.437)	0.95	6.23
<i>D. ocoee</i>	0.020	2.054 (1.793, 2.314)	0.450 (0.375, 0.525)	0.75	1.92
Coweeta					
<i>D. quadramaculatus</i>	0.064	1.298 (1.226, 1.369)	0.210 (0.195, 0.225)	0.95	30.90
<i>D. monticola</i>	0.034	2.030 (1.888, 2.171)	0.362 (0.330, 0.394)	0.88	9.26
<i>D. ocoee</i>	0.015	2.213 (2.013, 2.413)	0.442 (0.387, 0.497)	0.84	2.24

TABLE 3.—Relative growth rates (γ_i) in standard length (γ_{SL} in millimeters) and body mass (γ_M in grams) as a function of age (A in years), according to $\ln(\gamma_i) = \ln(\beta_i) - \alpha_i A$, in three species of *Desmognathus* at Wolf Creek and Coweeta, based on the Gompertz parameters given in Tables 1 and 2. Ages at the maximum rate of absolute growth (equal to relative growth rates of α_i) are listed under λ_{SL} and λ_M .

Population	$\ln \gamma_{SL}$	$\ln \gamma_M$	λ_{SL}	λ_M
Wolf Creek				
<i>D. quadramaculatus</i>	$\ln 0.517 - 0.269A$	$\ln 1.751 - 0.313A$	2.43	5.50
<i>D. monticola</i>	$\ln 0.660 - 0.366A$	$\ln 2.086 - 0.409A$	1.61	3.98
<i>D. ocoee</i>	$\ln 0.648 - 0.377A$	$\ln 2.054 - 0.450A$	1.44	3.37
Coweeta				
<i>D. quadramaculatus</i>	$\ln 0.489 - 0.243A$	$\ln 1.298 - 0.210A$	2.88	8.67
<i>D. monticola</i>	$\ln 0.642 - 0.333A$	$\ln 2.030 - 0.362A$	1.97	4.76
<i>D. ocoee</i>	$\ln 0.696 - 0.388A$	$\ln 2.213 - 0.442A$	1.51	3.64

ocoee and *D. monticola* were similar, and higher than in *D. quadramaculatus*. Given that the larval periods of *D. ocoee* and *D. monticola* are less than 1 yr, in contrast to the 3–4 yr larval phase of *D. quadramaculatus* (Bruce 2011:Table 1), the early differences were mainly between juveniles of *D. ocoee* and *D. monticola* and larvae of *D. quadramaculatus*. Although hatching sizes (SL_0 , M_0) were greater in *D. quadramaculatus* than in *D. monticola* (Tables 1, 2), the higher values of the initial relative growth rates (β_{SL} , β_M at age 0) of the latter generated similar age-specific body sizes of the two species in the early years of life in both assemblages. For example, for growth in SL from ages 2–3 yr, the values based on the Gompertz parameters were: Wolf Creek, 30.9–40.3 mm for *D. quadramaculatus*, 30.1–39.2 mm for *D. monticola*; Coweeta, 30.4–39.7 mm for *D. quadramaculatus*, 30.1–39.9 mm for *D. monticola*. Eventually, the greater rates of decay (α_{SL} , α_M) in the relative growth rates of *D. monticola* versus *D. quadramaculatus* led to the divergence in body size exhibited by the two species (as expressed in the asymptotic body sizes, SL_{max} and M_{max} ; Tables 1 and 2). Although the relative growth rates of *D. ocoee* were similar to those of *D. monticola* (Table 3), the smaller hatching sizes of the former (Tables 1 and 2) prescribed smaller sizes of *D. ocoee* versus *D. monticola* throughout life, and much smaller sizes than those of *D. quadramaculatus*. For example, in comparison with the values given above, increases in SL of *D. ocoee* from ages 2 to 3 yr were 23.5–30.2 mm at Wolf Creek and 24.3–31.7 mm at Coweeta. At Wolf Creek in particular, the plots of relative growth rate of SL against age of *D. ocoee* and *D. monticola* were nearly coincident (Fig. 1A); however, the initial difference in hatching sizes (9.4 vs. 11.8 mm in SL, respectively) provided for larger sizes of the latter species throughout the salamanders’ life spans.

In comparing the Wolf Creek and Coweeta populations of the three species, the plots of relative growth rate versus age

of *D. monticola* and *D. quadramaculatus* were both shifted upward at Coweeta versus Wolf Creek but were nearly coincident in *D. ocoee*. This is shown in the Gompertz plots of relative growth in SL and mass (Figs. 1 and 2) and the von Bertalanffy plot of relative growth in mass (Fig. 3). With respect to *D. ocoee*, the effect was more pronounced for *D. quadramaculatus* than in *D. monticola*.

The goodness of fits of the von Bertalanffy equations of absolute growth in mass (as reflected in the R^2 values; Table 4) were similar to those of the Gompertz equations (Table 2). In evaluating relative growth in mass, γ_M , I transformed the values to logarithms, and plotted the log-transformed values against age (Fig. 3). The graphs have a complex curvilinear form, as reflected in the fitted equations (Table 5), but the pattern of differences among species was similar to that of the Gompertz plots, with the larger species showing the higher rates of relative growth at older ages.

For growth in mass, the ages at the maximum rates of absolute growth ($\lambda_M =$ relative growth rates of α_M , and $\omega(1 - k)/k$, respectively) varied between the Gompertz and von Bertalanffy models (Tables 3 and 5), but were near or within ages at sexual maturation, as documented in Castanet et al. (1996) and Bruce et al. (2002). Between populations, these ages were greater at Coweeta than at Wolf Creek in both models. Differences between the populations of *D. ocoee* were minimal, however, as expected on the basis of the near coincidence of the plots of relative growth rates on age in this species (Figs. 1–3).

DISCUSSION

A large body of evidence indicates that intraguild predation and interspecific competition in *Desmognathus*, as well as interactions with other plethodontid salamanders, contribute to the organization of desmognathine assemblages

TABLE 4.—Von Bertalanffy parameters for growth in body mass (M in grams) for three species of *Desmognathus* at Wolf Creek and Coweeta, based on skeletochronological data sets reported in Castanet et al. (1996) and Bruce et al. (2002). Sample sizes as in Table 1; the 95% confidence limits are given in parentheses.

Population	M_{max}	ω	δ	k	R^2
Wolf Creek					
<i>D. quadramaculatus</i>	18.0	-1.572 (-2.021, -1.123)	-1.487 (-1.597, -1.378)	1.196 (1.158, 1.234)	0.88
<i>D. monticola</i>	8.5	-1.588 (-1.871, -1.304)	-1.297 (-1.363, -1.231)	1.215 (1.191, 1.239)	0.93
<i>D. ocoee</i>	1.95	-1.791 (-2.591, -0.991)	-2.905 (-3.298, -2.512)	1.323 (1.226, 1.419)	0.75
Coweeta					
<i>D. quadramaculatus</i>	29.0	-1.533 (-1.764, -1.302)	-1.138 (-1.192, -1.083)	1.151 (1.136, 1.165)	0.95
<i>D. monticola</i>	10.0	-1.541 (-1.922, -1.160)	-1.887 (-2.021, -1.753)	1.244 (1.205, 1.284)	0.88
<i>D. ocoee</i>	2.20	-1.950 (-2.493, -1.406)	-2.797 (-3.028, -2.565)	1.296 (1.241, 1.351)	0.84

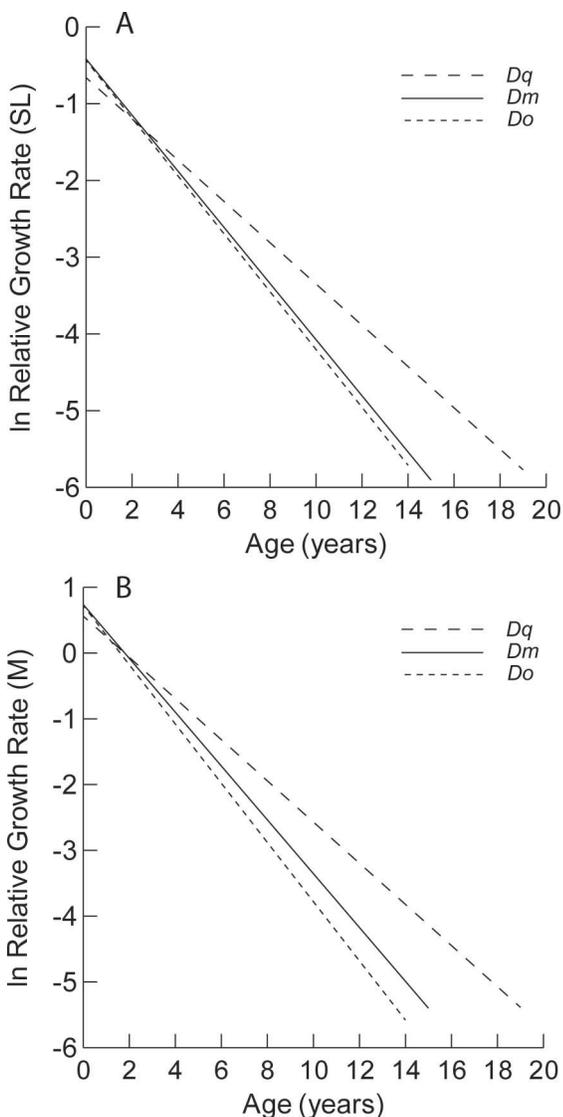


FIG. 1.—Decay of ln relative growth rate in (A) standard length and (B) body mass with age for Wolf Creek *Desmognathus*, based on Gompertz equations. *Dq* = *D. quadramaculatus*, *Dm* = *D. monticola*, *Do* = *D. ocoee*.

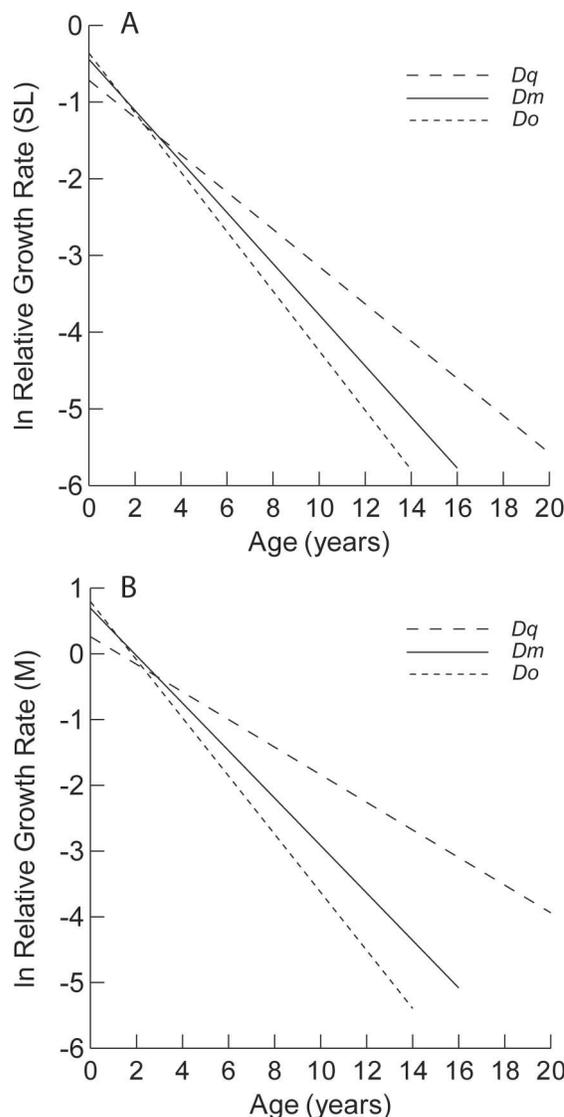


FIG. 2.—Decay of ln relative growth rate in (A) standard length and (B) body mass with age for Coweeta *Desmognathus*, based on Gompertz equations. *Dq* = *D. quadramaculatus*, *Dm* = *D. monticola*, *Do* = *D. ocoee*.

along the stream-to-forest habitat gradient in Appalachian ecosystems (reviewed in Hairston 1987, 1996; Bruce 2011). Generally, in multispecies communities of desmognathines, the larger species occur in streams and the smaller forms are progressively more terrestrial (but overlap is prevalent; Hairston 1987:Fig. 6.1; Petranka and Smith 2005:Fig. 3). Although ecological interactions might serve to reinforce the observed partitioning of habitat, a remaining question is the adaptive significance of the relationship between body size/morphology and habitat utilization. In the aquatic forms, larger sizes at hatching, lengthier larval phases, and larger metamorphic and adult sizes might promote effective purchase on the stream bottom, and efficient swimming and head-wedging beneath large rocks (Schwenk and Wake 1993). In contrast, smaller body sizes in more terrestrial species might allow for better use of forest floor resources such as retreats for foraging, protection, and nesting. Substrate choice experiments in *D. quadramaculatus*, *D.*

monticola, *D. ocoee*, and related species have demonstrated behavioral differences among species in substrate preference that are correlated with differences in body size and habitat utilization (Krzysik and Miller 1979; Carr and Taylor 1985; Southerland 1986).

Larger versus smaller body sizes, as adaptations to the physical environment, and mediated through biotic interactions, are attained by (1) larger propagule sizes, (2) higher growth rates, and (3) lower developmental rates (to sexual maturation) in *D. quadramaculatus* versus the smaller species, *D. monticola* and *D. ocoee* (Bruce 2010, 2016). The trend is also found in *D. ocoee* versus the smaller *D. aeneus* and *D. wrighti* (Bruce 2009, 2014). All three factors are expressed in the analyses of relative growth rate, but from a different vantage, given that plots of relative growth rate are not growth curves per se. Thus, in comparing the Wolf Creek and Coweeta populations of each species, the extent of shifts in the plots of relative growth rate versus age

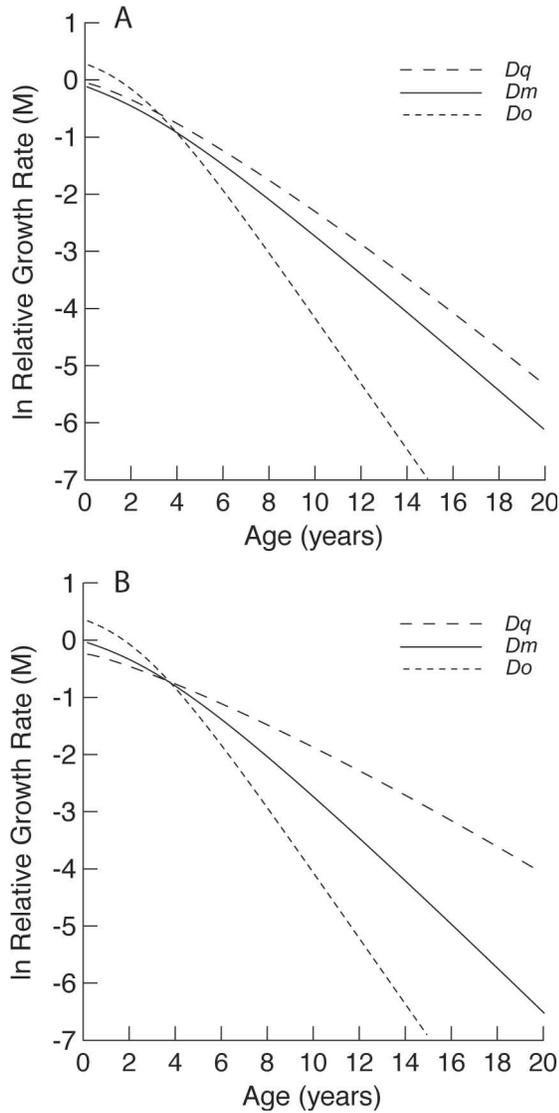


FIG. 3.—Decay of ln relative growth rate in body mass with age for (A) Wolf Creek and (B) Coweeta *Desmognathus*, based on von Bertalanffy equations. $D_q = D. quadramaculatus$, $D_m = D. monticola$, $D_o = D. ocoee$.

reflect the variation in adult body sizes, which are greater in Coweeta *D. quadramaculatus* and *D. monticola*, but nearly identical in the two populations of *D. ocoee* (Bruce 1990; Bruce and Hairston 1990; Castanet et al. 1996; Bruce et al. 2002; Bruce 2013).

Given the variation in growth expressed by point scatters in plots of size versus age (Bruce 2010, 2016), both the Gompertz and von Bertalanffy models provided reasonable approximations of growth trends in *Desmognathus*. Maxima of absolute growth rates in mass, equal to relative growth rates of α_M (Gompertz model) or $\omega(1 - k)/k$ (von Bertalanffy model), were somewhat higher under the latter model, but in both occurred near or within the reported age ranges at first reproduction (Castanet et al. 1996; Bruce et al. 2002). This conforms to the pattern in desmognathines and other salamanders of a slowing of growth at sexual maturation.

How such attributes of growth relate to other life-history traits remains uncertain. Although females of the faster-

TABLE 5.—Relative growth rates in mass (γ_M in grams) as a function of age (A in years), according to $\ln \gamma_M = \ln \left[\frac{\delta \omega}{1 - \delta e^{[-\omega(1 - k)A]}} \right] e^{[-\omega(1 - k)A]}$, in three species of *Desmognathus* at Wolf Creek and Coweeta, based on von Bertalanffy parameters (Table 4). Ages in years at the maximum rate of absolute growth are listed under λ_M . At the maximum rate of absolute growth, the relative growth rate is formulated from the parameters of Table 4 as $\gamma_M^* = \omega(1 - k)/k$.

Population	$\ln \gamma_M$	λ_M	γ_M^*
Wolf Creek			
<i>D. quadramaculatus</i>	$\ln \left[\left(\frac{2.3375}{1 + 1.487e^{(-0.3081A)}} \right) e^{(-0.3081A)} \right]$	6.58	0.258
<i>D. monticola</i>	$\ln \left[\left(\frac{2.0596}{1 + 1.297e^{(-0.3414A)}} \right) e^{(-0.3414A)} \right]$	5.26	0.281
<i>D. ocoee</i>	$\ln \left[\left(\frac{5.2028}{1 + 2.905e^{(-0.5785A)}} \right) e^{(-0.5785A)} \right]$	3.80	0.437
Coweeta			
<i>D. quadramaculatus</i>	$\ln \left[\left(\frac{1.7446}{1 + 1.138e^{(-0.2315A)}} \right) e^{(-0.2315A)} \right]$	8.70	0.201
<i>D. monticola</i>	$\ln \left[\left(\frac{2.9079}{1 + 1.887e^{(-0.3760A)}} \right) e^{(-0.3760A)} \right]$	5.44	0.302
<i>D. ocoee</i>	$\ln \left[\left(\frac{5.4542}{1 + 2.797e^{(-0.5772A)}} \right) e^{(-0.5772A)} \right]$	3.89	0.445

growing and later-maturing larger species have higher fecundity (Tilley 1968; Bruce 1996), such relationships do not express differences in female reproductive effort, given that the larger species produce larger eggs that yield larger hatchlings, in comparison with the smaller species (Orr and Maple 1978; Bruce 1990; Tilley and Bernardo 1993; Bernardo and Agosta 2003; Bruce 2009, 2014). For two populations of *D. ocoee* that are near the Wolf Creek and Coweeta populations, Bernardo (1994) reported differences in resource allocation in response to variation in acquisition (food supplementation) and environmental (mainly thermal) differences between the sites. Trade-offs involving variation in growth and reproductive effort, and the influence of other life-history and demographic traits, are incompletely documented in the desmognathine assemblages occurring in these areas (Bruce 2009, 2013, 2014). Moreover, the underlying genetic correlations are unknown (the complexities of trade-off analysis are reviewed in Roff and Fairbairn 2007). The expectation is that within a given assemblage the larger species of *Desmognathus*, that grow faster, mature later, and purportedly have higher survival in comparison to their smaller congeners (Bruce 2013), would continue to have lower reproductive effort at later ages, as measured by the ratio of clutch mass to body mass or some other appropriate metric.

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